

Why Evolution Is True

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The demise of group selection

The idea that adaptations in organisms result from “group selection” (selection among groups that differentially bud off subgroups, with those having good “group traits” becoming more numerous), rather than from selection among genes themselves, usually within individuals, has undergone a bit of resurgence in popular culture. This is in stark contrast to the views of most evolutionary biologists, who see group selection as a *logical* possibility, but one that doesn’t easily work in theoretical models and, more important, has explained almost nothing about nature. In contrast, the gene-centered view of evolution worked out by biologists like W. D. Hamilton, Robert Trivers, and John Maynard Smith, and popularized by Richard Dawkins, has been immensely fruitful.

I’ve posted a lot on the intellectual vacuity of group selection, particularly its failure to explain the evolution of traits like human altruism and cooperation (see, for example, [here](#), [here](#), and [here](#)). If you want an elegant and easily digestible explanation of the weaknesses of group selection, Steve Pinker has just published a nice essay on John Brockman’s *Edge* website, “[The false allure of group selection](#).” If you’re interested in seeing three smart biologists take group selection apart, there’s [an excellent paper by West, Griffin, and Gardner](#) (reference below), which you can download for free [here](#) (the paper is not too hard, and the meat extends from pp. 376, beginning at “Error 3: the new”, to p. 379, bottom of Table 2).

There are several reasons why group selection has waned in popularity among evolutionists:

- Group selection is a fuzzy and nebulous concept that is far less coherent than is gene-level selection (see Pinker’s essay for an explanation)
- As I said above, when group selection *does* work in theory, it can be shown to be mathematically equivalent to gene-level selection involving “inclusive fitness.” But the group-selection scenarios are far more unwieldy, and are often so complex that they can’t be modeled. As West et al. note:
 1. “No group selection model has ever been constructed where the same result cannot be found with kin selection theory”.
 2. “The group selection approach has proved to be less useful than the kin selection approach.”
 3. “The application of group selection theory has led to much confusion and time wasting.” It is, as the authors say, “easy to misapply, leading to incorrect statements about how natural selection operates,” it is “not distinct from kin selection”, and it “often leads to the confusing redefinition of terms and the use of confusing jargon.”
- There are formidable theoretical problems with many concepts of group selection. These include the fact that individuals reproduce faster than groups, so that an adaptation that is good for groups (say, pure altruism, in which individuals sacrifice their reproduction through behaviors that bring no benefits to the genes producing such behaviors), won’t spread because the rate of propagation of groups is undermined by the evolutionary *disadvantage* of altruistic behaviors within groups (non-altruists, or “cheaters,” will replace the altruists

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since they get the benefits without the costs). In other words, altruistic groups may do better than non-altruistic ones, but that won't produce species-wide altruism because non-altruists do better than altruists *within* groups—unless, of course, altruists aren't "pure" altruists and their genes reap some benefit from the behavior, in which case it's kin selection.

- While logically and theoretically possible, when group selection *does* work it can be shown to be equivalent to gene-level selection, usually acting through interactions between individuals. It is thus more fruitfully modeled—and explained—by gene- and individual-centered explanations that often involve "inclusive fitness" (IF). IF is the idea that genes can gain a benefit not just by increasing the reproductive output ("fitness") of individuals themselves, but via the interaction of those individuals with relatives or members of their group who carry the same genes. Human "altruism," for example, is explained more parsimoniously by kin-selected IF models or other gene-centered approaches like reciprocal altruism ("I'll scratch your back if you'll scratch mine")—or, in primates, by the notion that "altruistic" acts actually increase fitness by giving a good reputation to the altruist. Further, the data from nature show that the way altruism and cooperation operate in animals is more consistent with their evolution by gene- and individual-level selection than by group selection (see [here for an explanation](#)).
- Finally, I am not aware of a single adaptation in nature that can be explained better by group selection than by kin selection. (A single possible exception is the evolution of sexual reproduction, but we still know very little about how sex evolved.) In contrast, as the West et al. paper notes (see Table 1), as well as [several responses to a 2010 Nature paper by Nowak et al. dissing kin selection](#), kin-selection theory and its underlying concept of inclusive fitness have been immensely fruitful in understanding the evolution of social behavior. It is kin selection and not group selection that has helped us understand things like sibling conflict, sex ratios in social insects and parasites, parent-offspring conflict, and genomic imprinting. Group selection has had no such success. A stark example of the impotence of the group-selection approach is given by West et al. (p. 378):

. . . [W. D.] Hamilton's original model has been extended in numerous directions to match the biology of particular organisms, allowing more specific tests of theory (Frank, 1998; West et al., 2005). This allows us to quantify the relative use of the group selection and kin selection approaches, by examining the relative frequency with which these methods led to new areas of theory that could be empirically tested. We have performed this, and found that in 15 of 15 cases, it was kin selection theory that was used (Table 2; $P = 0.00006$, two-tailed sign test). Sex-ratio theory therefore provides clear statistical support for the usefulness of kin selection over group selection.

So if group selection is so intellectually and scientifically unproductive, why do we hear so much about it? I think there are two reasons.

First, its few proponents make a lot of noise. And those proponents include well-known scientists like Martin Nowak, E. O. Wilson, David Sloan Wilson, and Jon Haidt. Nowak, Tarnita, and Wilson published a big (and deeply faulty) paper in *Nature* asserting that group selection was a better explanation than kin selection for "eusociality": the social system of animals, like bees and ants, that have sterile "castes" of workers that divide up colony labor, and have one or a few fertile queens tended by those workers. (For links, see [my post on the scientific community's rejection of that paper](#).) Wilson has incorporated many of these erroneous ideas into a new book, *The Social Conquest of Earth*, that will, because of Wilson's prominence, be widely read by the public. (I hasten to add that his other biological work has usually been superb.) Wilson's book has not received much acclaim from scientists: it's been severely criticized, for example, by [Steven Mithen](#) in *The New York Review of Books* and by [Richard Dawkins](#) in *Prospect*. I'll be weighing in on the book later.

Jonathan Haidt, another well-known psychologist with a wide public following, has also pushed the group selection in his new book *The Righteous Mind*. I've previously critiqued his TED talk on the book, and Haidt's penchant for group-selection explanations of religion and human cooperation, [here](#).

The problem with all this is that the arguments for group selection are being made in books aimed at the general public, but the critical responses by evolutionary biologists are not only buried in technical papers, but involve arcane scientific arguments that sometimes use (horrors!) *mathematics*. So while group selection may flourish in the public mind, it's moribund to most evolutionary biologists who have followed the technical debates in the literature.

Second, people *want* to believe in group selection. That doesn't just include scientists like D. S. Wilson, who has made it his life's mission to defend the concept, but more importantly by the general public. We want to think that stuff like religion, cooperation, and altruism have spread by group selection because that involves the concept of harmonious and cooperating groups. Such a notion is deeply appealing to those who have a dislike for the idea of the "selfish gene," mistakenly conflating that notion with the idea of selfish *individuals*. As all evolutionists know, or should know, cooperation and altruism can evolve *via* selfish genes!

Nevertheless, the idea of group-level adaptations has an innate appeal to those with a penchant for the religious and the spiritual. Why, just this morning the unctuous Krista Tippett (why *do* people listen to her?) [interviewed D. S. Wilson](#) on her "On Being" show on National Public Radio. The topic was Wilson's attempts to improve his own city of Binghamton, New York using evolutionary principles of group selection. Last year, [in a review of Wilson's book *The Neighborhood Project* in *The New York Times*](#), I strongly criticized his evolutionary-based sociology.

So while group selection is moribund among evolutionary biologists and many evolutionary psychologists, the criticisms of the idea are buried in the technical literature while its vocal proponents write best-selling books. Behind much of this is the insidious Templeton Foundation, which has for some reason decided to promote group selection, probably because of its religious and spiritual connections and its link to "goddy" things like altruism and cooperation. Both D. S. Wilson and Martin Nowak, for example, are heavily funded by Templeton. And Jon Haidt not only was funded by two Templeton grants ([here](#) and [here](#)), but they also funded a sabbatical semester for him to write a book in 2003. Plus he won the Templeton Prize for Positive Psychology in 2001. (I guess there's no prize for Negative Psychology.)

With all that money and all those megaphones behind it, the idea of group selection persists in the public mind while slowly dying in the scientific community. Yes, it's dying, but it refuses to lie down.

West, S. A., A. S. Griffin, and A. Gardner. 2007. [Social semantics: how useful has group selection been?](#) *J. Evol. Biol.* 21: 374-385; doi: 10.1111/j.1420-9101.2007.01458.x.

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23 Comments



1.

Ken Pidcock

Posted June 24, 2012 at 9:17 am | [Permalink](#)

It might be helpful to provide a link to Nowak et al. [itself](#), so that people can judge for themselves just how deeply flawed it is. Or are we, perhaps, assumed to be unable to do that?

Reply



whyevolutionistrue

Posted June 24, 2012 at 9:24 am | [Permalink](#)

Look, there's no need to be snarky; I simply forgot the link, but I've added it now.

Take a grumpy pill this a.m.?

Reply



Ken Pidcock

Posted June 24, 2012 at 10:14 am | [Permalink](#)

I apologize for my impertinence, but it has been my perception that too much of the discussion on this topic has excluded reference to what, specifically, those authors were saying.

Reply



whyevolutionistrue

Posted June 24, 2012 at 10:18 am | [Permalink](#)

Umm. . . if you check my previous discussions on this topic (see references given in the post), you'll see that I not only link to what I'm discussing, but summarize what it says.

Reply



tryangregory

Posted June 24, 2012 at 12:16 pm | [Permalink](#)

The title of the West et al paper is not (as cited above)

"Social semantics: how useful has group selection been?"

it is

"Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection"

Reply



whyevolutionistrue

Posted June 24, 2012 at 12:37 pm | [Permalink](#)

Sorry! I put in a link to the wrong paper. I've now fixed it, and thanks for the alert.

-C.C.

Reply



tryangregory

Posted June 24, 2012 at 12:20 pm | [Permalink](#)

Here's the link to the paper with the title cited above:

http://www.life.umd.edu/faculty/wilkinson/BIOL608W/WestGriffinGardner_08.pdf

Reply



tryangregory

Posted June 24, 2012 at 12:21 pm | [Permalink](#)

(The current link is to a different paper, with the title "Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection".)

Reply



sciencebulldog

Posted June 24, 2012 at 9:48 am | [Permalink](#)

Forgive my ignorance as I try to wrap my head around this fascinating discussion of group vs. kin selection. It seems to me that with kin selection you always have a "direct" connection to lineage, while in group selection you do not. Thus over time natural selection can "process" kin as genes are directly passed down, while groups are not likely to be connected over a sufficient amount of time for this to occur. The inherit noise in differing groups over time would outweigh most gradual selection effects that would be able to continue through the genetic lineage of kin. Does this make sense or am I way off? I still am reading up on the topic.

Reply



Ken Pidcock

Posted June 24, 2012 at 9:59 am | [Permalink](#)

Here's a very good and concise [defense](#) of inclusive fitness theory, specifically against Nowak et al.

Bourke, A. F. 2011. The validity and value of inclusive fitness theory. Proc Biol Sci 278:3313-20.

Reply



gbjames

Posted June 24, 2012 at 10:27 am | [Permalink](#)

sub

Reply



Achrachno

Posted June 24, 2012 at 10:35 am | [Permalink](#)

Is species selection not a form of group selection? It does seem to be

the case that when a whole species goes down, perhaps due to the invasion of its range by a competitor or predator, even the best adapted genotypes within it are going to disappear too. Passenger pigeons all went away under heavy shooting pressure in a few decades. There apparently wasn't time for natural selection to create a new model better adapted to the changed conditions — despite the probability that some were more wary, quicker, or more tolerant of small group size. Likewise, in a major crisis (e.g., Permian organic crisis) whole clusters of species and larger clades can be wiped out regardless of the influence of normal gene-based selection. Why can't selection operate at multiple levels, at least sporadically?

Reply



6.

Cooperator

Posted June 24, 2012 at 10:49 am | [Permalink](#)

Two quick comments.

1) The idea that group selection and kin selection are mathematically equivalent is false. The persistence of this idea is really amazing since it doesn't even make sense intuitively. See van Veelen "Group selection and kin selection are not mathematically equivalent" (2012) *Journal of theoretical biology*, for what should be (but won't be) the end of that idea.

2) Group selection can work just fine even if groups survive for much longer than one generation of individuals before "budding" or "fissioning". Does anybody know where this idea originates? It isn't even close to being true. There are some new animations of solutions of the dynamical equations for two-level population processes posted on youtube

This should prove that groups can live much longer than individuals without preventing group selection.

There are other problems with Jerry's post, but these are two that stand out because they are such common misconceptions.

Reply



Occam

Posted June 24, 2012 at 11:44 am | [Permalink](#)

Could you please post the equations, or generally accessible links to them? Thanks.

Reply



Cooperator

Posted June 24, 2012 at 12:11 pm | [Permalink](#)

Here's a paper that's already published

<http://www.math.ucdenver.edu/~bsimon/EER%20journal%20version.pdf>

There's newer stuff that's probably better. Send me an email for more info. Jerry gets mad when I blow my horn on his website 😊

Reply



Ryan

Posted June 24, 2012 at 12:12 pm | [Permalink](#)

Here is a response to the van Veelen paper and others that I believe is open access.

<http://onlinelibrary.wiley.com/doi/10.1111/j.1420-9101.2012.02498.x/full>

Reply



o

whyevolutionistrue

Posted June 24, 2012 at 12:35 pm | [Permalink](#)

PLEASE do not embed videos in the comments!

Reply

7.



bestss

Posted June 24, 2012 at 10:59 am | [Permalink](#)

A false idea relentlessly and shamelessly promoted becomes "fact."

Paradoxically, the lie of group selection is immoral in it's campaign of spreading a falsehood.

Lies in the service of "morality!?"

Reply

8.



riffingreligion

Posted June 24, 2012 at 11:19 am | [Permalink](#)

It's been a while since I read any of the proponents of group selection, but I recall it making little sense for genetic traits, while seeming more plausible when tackling cultural traits. It's at least more plausible than "memes", which I see as a failed attempt to treat cultural evolution as a direct analogue of biological evolution. A priori, there's no reason to think that the explanation for why Christian churches proliferated while other contemporary religions like Manicheanism languished in obscurity should have to be the same as the genetic explanation of how homo sapiens spread across the world while other homo species died out.

None of this is to say that group selection in cultural evolution is

right. It still has many of the same problems (defining the unit of selection, for example). But given that the mechanisms of cultural evolution are still very poorly understood (unlike biological evolution), I wouldn't rule it out. Of the serious proposals for cultural evolution that I've heard, group selection is not the most unlikely (again, that would be memes).

[Reply](#)



9.

[sciencecmd68](#)

Posted June 24, 2012 at 11:22 am | [Permalink](#)

Group selection seems to arise to explain seemingly maladaptive traits like altruism or senescence. But group selection absolutely is not necessary if you have recessive gene. Traits, like sickle cell disease can be maladaptive for some, but beneficial for individuals with only one copy. If altruism were like sickle cell disease we would not need group selection to explain it. Those with one copy of the gene would not be terribly altruistic and would not decrease their fitness significantly. Those with two copies would be altruistic, and though their fitness might suffer, the allele for altruism would thrive in those with their only one copy, who would be aided in survival by their altruistic brethren. So long as the heterozygotes had improved survival over those without the allele in the gene pool, the allele would take off.

[Reply](#)



10.

Jim Thomerson

Posted June 24, 2012 at 11:25 am | [Permalink](#)

A catastrophe happens so intensely or so rapidly that no members of a population survive. When this happens, the previous pre catastrophe variation in fitness of individuals is rendered irrelevant.

[Reply](#)



11.

caf

Posted June 24, 2012 at 11:59 am | [Permalink](#)

Dr. Coyne and Readers:

Have any of you seen this article in Sunday Times (London) :

<http://www.bryanappleyard.com/not-in-our-genes/>

[Reply](#)



12.

[emmageraln](#)

Posted June 24, 2012 at 12:42 pm | [Permalink](#)

Reblogged this on [emmageraln](#).

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1. By [Group selection and Jerry Coyne](#) < [Mathematical Biology](#) on June 24, 2012 at 9:57 am

[...] Jerry A. Coyne continues to express his opinion on the group selection concept in his blog. [...]

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